REVALIDATION OF *LAMPANYCTUS GEMMIFER* (GOODE & BEAN, 1879), A JUNIOR SYNONYM OF *LAMPANYCTUS CROCODILUS* (RISSO, 1810) IN THE ATLANTIC OCEAN (MYCTOPHIDAE)

by

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ABSTRACT. - A taxonomic study of 147 examples previously classified as *Lampanyctus crocodilus* (Risso, 1810), captured both in the North Atlantic and in Mediterranean Sea, has revealed the existence of an unvarying series of meristic deviations between Mediterranean and Atlantic populations. The most important differences are found in gillraker and AOa photophore counts, but there are also slight differences in dorsal and anal fin ray counts. The absence of clinal variation in the above mentioned meristic characters, even between specimens collected in the neighbouring areas of the Gulf of Cadiz and the Alboran Sea, seems to indicate a lack of genetic interchange between Atlantic and Mediterranean populations through the Strait of Gibraltar. In the light of these results we propose Atlantic specimens belong to the species *Lampanyctus gemmifer* (Goode & Bean, 1879), a similar but different species from L. *crocodilus*, previously described from the Northwestern Atlantic. *L. crocodilus* is herein restricted to the Mediterranean.

RÉSUMÉ. - L'étude taxonomique de 147 exemplaires répertoriés jusqu'à présent comme *Lampanyctus crocodilus* (Risso, 1810), capturés dans l'Atlantique nord et en Méditerranée, a montré l'existence de différences méristiques constantes entre les populations atlantiques et méditerranéennes. Les différences les plus importantes se trouvent dans le nombre de branchiospines du premier arc branchial et dans le nombre de photophores AOa, mais aussi dans le nombre de rayons des nageoires dorsale et anale. L'absence de variation clinale entre les exemplaires capturés dans le Golfe de Cadix et la Mer d'Alboran montre l'absence d'un échange génétique entre les populations atlantiques et méditerranéennes par le détroit de Gibraltar. Enfin, les résultats obtenus permettent de considérer que les spécimens atlantiques appartiennent à l'espèce *Lampanyctus gemmifer* (Goode & Bean, 1879), très proche de *L. crocodilus* décrite auparavant de l'Atlantique nord-ouest.

Key-words. - Myctophidae, *Lampanyctus gemmifer*, *Lampanyctus crocodilus*, AN, MED, Taxonomy.

Lampanyctus crocodilus was first described by Risso (1810) as *Gasteropelecus crocodilus*, from material taken off the coast of Nice. The description however, was not very accurate and no reference to the photophores or the gillrakers was included. Furthermore it was unaccompanied by iconography and there was no designation of type material.

Following Risso's work, *L. crocodilus* has been recorded from the Mediterranean on several occasions (cf. Krefft and Bekker, 1973), where it is a common species, and also from the North Atlantic (e.g., Lütken, 1892; Brauer, 1904; Holt and Byrne, 1906, 1911; Tåning, 1928).

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Moreover, Parr (1929) considered that *Lampanyctus gemmifer* (Goode & Bean, 1879), described from the Northwestern Atlantic (type locality: 39° 39'45"N, 71° 35'15"W) was, in fact, a synonym of *L. crocodilus*. The taxonomic similarity between both species had already been noted by Goode and Bean (1896) and Parr (1929: 27) latterly wrote: "An inspection of the above type specimen reveals the perfect identity of Goode and Bean's species with *L. crocodilus* already described by Risso in 1810 [1910 in the original], as clearly shown on the accompanying diagram. Three photophores are found on each cheek, in the arrangement typical of *L. crocodilus* and a luminous scale is present in the adipose fin". Since Parr's paper, *L. gemmifer* has been considered a junior synonym of *L. crocodilus* (e.g., Krefft and Bekker, 1973).

Interestingly, however, Holt and Byrne (1906: 14) had already questioned the identity of their studied material taken from the North Atlantic: "It will be seen that while closely approaching several species our specimens do not exactly agree with the descriptions of any, and it is only by comparison with the British Museum material of *S. crocodilus* that we have felt able to refer them to that species. The Museum series consists of a number of Mediterranean examples of different sizes". Furthermore, these authors mentioned another example of *L. crocodilus* taken from the stomach of one fish from the Atlantic (off the Azores), that really corresponds to *Lampanyctus intricarius*, a closely related species described by Tåning (1928) a few years later.

L. crocodilus has been misidentified as *L. intricarius* on other occasions. For example, Stefanescu *et al.* (1993) have demonstrated that the only specimens recorded as *L. intricarius* from the Mediterranean Sea (Allué and Rubiés, 1984) were, in fact, *L. crocodilus*. This confusion was in part attributable to the meristic differences between the Mediterranean and presumed Atlantic populations of *L. crocodilus*, hindering a correct interpretation of the keys based on Atlantic material (e.g., Hulley, 1984).

To explore in greater depth the possible geographical differentiation of *L. crocodilus*, a detailed taxonomic investigation of both Atlantic and Mediterranean populations of supposed *L. crocodilus*, was instigated.

MATERIAL AND METHODS

For the present study 147 specimens identified as *L. crocodilus* were examined. This material came from different sites in the North Atlantic Ocean and Mediterranean Sea and formed part of the following museum collections: Natural History Museum (London), Muséum National d'Histoire Naturelle (Paris), Zoologisk Museum (Copenhagen), Institut für Seefischerei (Hamburg), Museum of Comparative Zoology (Harvard), South African Museum (Cape Town) and Institut de Ciències del Mar (Barcelona). Data from the holotype of *L. gemmifer*, deposited in the National Museum of Natural History (Washington D.C.), were kindly provided by Dr. Collette.

To enable comparison between Atlantic and Mediterranean specimens, the material was divided into four groups (Fig. 1): Northwestern Mediterranean (40° N to 42° N, 01° E to 03° E), Alboran Sea (36° N to 37° N, 02° W to 04° W), Northeastern Atlantic (14° N to 54° N, 08° W to 32° W) and Northwestern Atlantic (38° N to 41° N, 65° W to 71° W). The number of individuals, mean standard length and range of standard lengths in each group, are summarized in table I.

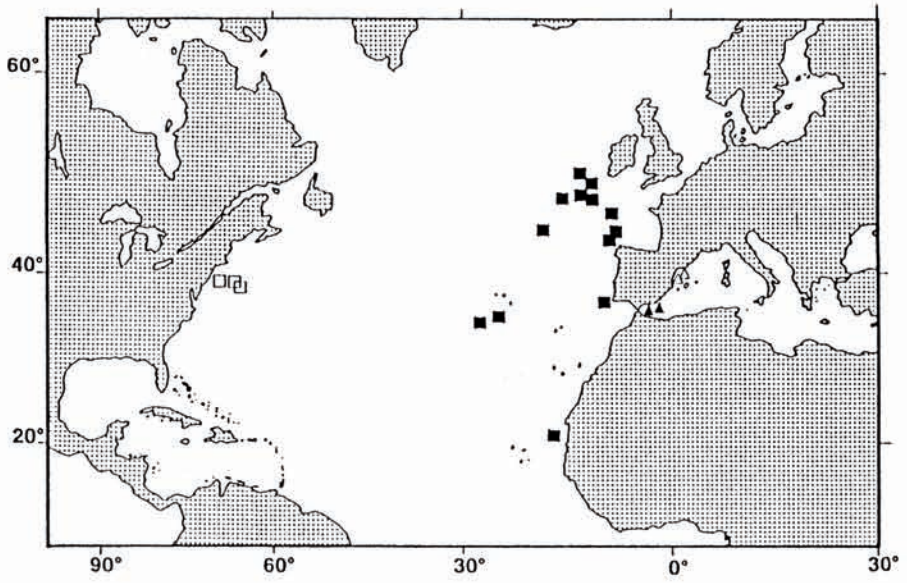

Fig. 1. - Map showing the localities from which material has been studied. Δ Northwestern Mediterranean; ▲ Alboran Sea; ■ Northeastern Atlantic; ❑ Northwestern Atlantic.

Studied material

Institutional abbreviations follow Leviton *et al.* (1985). To this list it is necessary to include that corresponding to the Fish Collection of the Institut de Ciències del Mar (Collection: IIPB).

Northwestern Mediterranean

BMNH 1976.7.30.26-33, Banyuls-sur-Mer, 8 ex.; BMNH 88.6.15.13, Nice, 1 ex.; BMNH, non catalogued, Mediterranean sea, 2 ex.; BMNH 85.7.1.2-3, Nice, 2 ex.; IIPB 190/1982, Catalan Sea, 1 ex.; IIPB 191/1982, Catalan Sea, 1 ex.; IIPB 192/1982, Catalan Sea, 1 ex.; IIPB 193/1982, Catalan Sea, 1 ex.; IIPB 194/1982, Catalan Sea, 1 ex.; IIPB, non catalogued, 40° 43'N-02° 41'E, 1 ex.; IIPB, non catalogued, 41° 05'N- 02° 26'E, 1 ex.; IIPB, non catalogued, 40° 48'N-02° 48'E, 1 ex.; IIPB, non catalogued, 41° 06'N-02° 09'E, 1 ex.; IIPB, non catalogued, 40° 55'N-02° 07'E, 2 ex.; IIPB, non catalogued, 40° 54'N-02° 05'E, 1

Table I. - Number of specimens, mean standard length and range of standard lengths of the four different groups considered in the present study.

	Number of specimens	Mean SL (mm)	Range SL (mm)
Northwestern Mediterranean	37	117.9	37.0 - 204.5
Alboran Sea	26	82.1	49.8 - 145.0
Northeastern Atlantic	44	86.4	22.2 - 156.4
Northwestern Atlantic	40	42.7	31.6 - 74.5

ex.; IIPB, non catalogued, 40° 55'N-02° 06'E, 2 ex.; IIPB, non catalogued, 41° 15'N-02° 28'E, 1 ex.; IIPB, non catalogued, 41° 11'N-02° 23'E, 2 ex.; IIPB, non catalogued, 40° 56'N-01° 34'E, 2 ex.; IIPB, non catalogued, 40° 54'N-01° 31'E, 1 ex.; IIPB, non catalogued, 40° 57'N-01° 33'E, 4 ex.; IIPB, non catalogued, 40° 52'N-01° 33'E, 1 ex.

Alboran Sea

IIPB, non catalogued, 33° 42'N-02° 20'W, 12 ex.; IIPB, non catalogued, 36° 30'N-02° 12'W, 5 ex.; IIPB, non catalogued, 36° 41'N-03° 15'W, 1 ex.; IIPB, non catalogued, 36° 36'N-02° 30'W, 2 ex.; IIPB, non catalogued, 36° 34'N-02° 41'W, 5 ex.

Northeastern Atlantic

BMNH 1972.1.26.17-28, 51° 40'N-13° 36'W, 8 ex.; BMNH 1934.12.19.9, 47° 66'N-8° 11'W, 1 ex.; MNHN 1980-1352, 44° 56'N-22° 00'W, 4 ex.; MNHN 1987-416, 53° 56'N-17° 50'W, 1 ex.; MNHN 1987-418, 36° 47'N-27° 21'W, 1 ex.; MNHN 1987-419, 37° 37'N-10° 06'W, 2 ex.; MNHN 1987-421, 46° 51'N-08° 38'W, 1 ex.; MNHN 1990-1036, 50° 15'N-13° 14'W, 1 ex.; MNHN 1990-1040, 47° 27'N-09° 35'W, 1 ex.; ISH 11-1966, 44° 13'N-08° 38'W, 4 ex.; ISH 25-1968, 43° 49'N-08° 58'W, 2 ex.; ISH 905-1974, 14° 11'N-18° 28'W, 2 ex.; ISH 2519-1979, 35° 23'N-31° 51'W, 1 ex.; SAM 29248, 47° 42'N-09° 08'W, 6 ex.; SAM 29540, 49° 59'N-20° 06'W, 6 ex.; ZMUC P2329375, 43° 49'N-08° 58'W, 1 ex.; ZMUC P2329376, 43° 49'N-08° 58'W, 1 ex.; ZMUC P2329378, 43° 49'N-08° 58'W, 1 ex.

Northwestern Atlantic

MCZ 98573, 39° 54'N-67° 42'W, 7 ex.; MCZ 98574, 40° 15'N-66° 07'W, 10 ex.; MCZ 98576, 39° 26'N-65° 42'W, 6 ex.; MCZ 98577, 39° 37'N-65° 49'W, 1 ex.; MCZ 98579, 38° 43'N-71° 57'W, 16 ex.

For each specimen the following meristic characters were analyzed: dorsal, pectoral and anal fin rays, gillrakers on the first gill arch (the whole arch including the raker in the angle and the upper and lower arms excluding the raker in the angle) and AO photophores (both AOa and AOp). These characters are the most utilized in taxonomic studies in the family Myctophidae and, moreover, they are most likely to show geographic variation (Badcock, 1981). For statistical inter-group analysis of the different meristic characters, Scheffé's linear contrast was followed (Scheffé, 1959).

RESULTS AND DISCUSSION

The results of the study of meristic traits are detailed in tables II, III and IV. Significant differences ($p < 0.01$) can be appreciated between the Atlantic and Mediterranean specimens for most of them, being particularly striking for the gillrakers and AOa photophores. For these characters Mediterranean specimens show significantly different values ($p < 0.01$) to those of the Northeastern and Northwestern Atlantic. Moreover, Mediterranean examples had higher dorsal fin-ray values but differences were only significant with respect to the Northeastern Atlantic group. Such marked differences were not observed for the other features (pectoral and anal fin rays and AOp photophores).

Considering the analyzed characters as a whole, a reliable separation of the Atlantic from the Mediterranean samples can be made. Thus using upper and lower gillrakers counts alone, 93% of the studied specimens could be correctly identified, while the number of total gill rakers correctly identified 88% and the number of AOa photophores 84% of all the 147 specimens analyzed (see Tables III and IV).

Differences are great enough to cause errors in identification when keys based on the presumed Atlantic *L. crocodilus* are used (e.g., Hulley, 1981; 1984). Thus, for example, the gillrakers number on the first gill arch coincides in Mediterranean specimens with that of the closely related *L. intricarius*. To avoid confusion, the position of the AOa_{1-2}

Table II. - Frequency distribution data and mean value of fin ray counts in the four geographical groups considered in the present study. Dorsal fin rays: differences are significant ($p < 0.01$) between Northwestern Mediterranean (NWM) and Northeastern Atlantic (NEA) and between Alboran Sea (AS) and NEA. Anal fin rays: differences are significant ($p < 0.01$) between NWM and NEA and between AS and NEA.

	Dorsal fin rays							Pectoral fin rays					Anal fin rays					
	12	13	14	15	16	x	n	13	14	15	x	n	16	17	18	19	x	n
Northwestern Mediterranean	-	1	20	15	1	14.4	37	3	14	2	14.0	19	-	7	26	2	17.9	35
Alboran Sea	-	2	10	14	-	14.6	26	3	22	-	13.9	25	-	7	18	-	17.7	25
Northeastern Atlantic	1	8	33	2	-	13.8	44	8	22	4	13.9	34	4	28	12	-	17.2	14
Northwestern Atlantic	-	3	28	9	-	14.2	40	1	23	12	14.3	36	-	23	16	-	17.4	39

Table III. - Frequency distribution data and mean values of meristic counts in the four geographical groups considered in the present study. Gillrakers of first arch (total, upper and lower arms): differences are significant ($p < 0.01$) among Northwestern Mediterranean (NWM) and Northeastern Atlantic (NEA), NWM and Northwestern Atlantic (NWA), Alboran Sea (AS) and NEA, AS and NWA.

	Gillrakers 1st arch																
	Total							Upper arm				Lower arm					
	14	15	16	17	18	x	n	4	5	x	n	9	10	11	12	x	n
Northwestern Mediterranean	5	28	4	-	-	15.0	37	35	2	4.1	37	5	30	2	-	9.9	37
Alboran Sea	2	24	-	-	-	14.9	26	26	-	4.0	26	2	24	-	-	9.9	26
Northeastern Atlantic	-	1	6	29	8	17.0	44	4	40	4.9	44	-	5	31	8	11.1	44
Northwestern Atlantic	-	1	5	33	1	16.9	40	4	36	4.9	40	-	4	35	1	10.9	40

photophores, the number of AOa photophores and the number of anal fin rays also need to be considered (Stefanescu *et al.*, 1993). Conversely, the number of gillrakers is sufficient to separate the presumed Atlantic *L. crocodilus* from *L. intricarius*.

In the authors' opinion, the observed differences between the Atlantic and Mediterranean populations are of sufficient magnitude to consider them two distinct species. The Mediterranean specimens would correspond to the species *L. crocodilus* first described by Risso (1810), and the Atlantic specimens to the species *L. gemmifer* originally described by Goode and Bean (1879) and subsequently considered to be a synonym of *L. crocodilus* by Parr (1929).

Whether *L. crocodilus* and *L. gemmifer* are distinct species or could be considered just as subspecies is obviously open to a degree of subjectivity. Such is the case, for example, with Atlantic and Mediterranean populations of the myctophid *Notoscopelus elongatus*, considered to belong to two different subspecies by Nafpaktitis (1975). However, the finding of sympatric specimens just west the Strait of Gibraltar (from where no specimens have been studied) would show that the two forms of *Lampanyctus* do live together, providing conclusive proof that no gene flow is occurring.

It has been suggested that AO photophores and dorsal and anal fin rays may be linked characters associated with the development of the myomeres during larval transformation (P.A. Hulley, pers. comm.), and therefore dependent on factors such as environmental temperature and salinity. Certain biogeographical details, however, strengthen a specific distinction between *L. crocodilus* and *L. gemmifer*. Firstly, the differences found between the Atlantic and Mediterranean specimens cannot be attributed solely to phenotypic variations produced by distinct environmental conditions during ontogenic larve development. Temperature and salinity differences between some of the North Atlantic sites studied (Fig. 1) are greater than those existing between the Alboran Sea (Southwest Mediterranean) and the Gulf of Cadiz (Northeastern Atlantic). In fact, the model of oceanic circulation through the Strait of Gibraltar (cf. Hopkins, 1985) describes a column of Atlantic water (temperature 15-17° C and salinity 36.15-36.5 ppt) occupying the first 150-200 m which enters and subsequently disperses over the Western Mediterranean Basin. Beneath this flows a countercurrent consisting of the so-called deep Mediterranean water (temperature 12.8° C and salinity 38.4 ppt).

Table IV. - Frequency distribution data and mean value of meristic counts in the four geographical groups considered in the present study. AOa photophores: differences are significant ($p < 0.01$) among Northwestern Mediterranean (NWM) and Northeastern Atlantic (NEA), NWM and Northwestern Atlantic (NWA), Alboran Sea (AS) and NEA, AS and NWA. AOp photophores: differences are significant ($p < 0.01$) among AS and NEA, AS and NWA.

	AO anterior					AO posterior					
	6	7	8	x	n	7	8	9	10	x	n
Northwestern Mediterranean	4	26	5	7.0	35	7	17	4	1	8.0	29
Alboran Sea	-	24	2	7.1	26	10	15	-	-	7.6	25
Northeastern Atlantic	34	8	-	6.2	42	7	21	9	3	8.3	40
Northwestern Atlantic	29	11	-	6.3	40	1	23	11	-	8.3	35

Secondly, the existence of a genetic interchange between the Atlantic and Mediterranean populations through the Strait of Gibraltar can be discounted given the total absence of a clinal variation in meristic characters, even between specimens collected in the neighbouring areas of the Gulf of Cadiz and Alboran Sea. This interchange would be perfectly feasible if both populations were the same species, given the vertical distribution and diel migrations observed in the first development stages (Tåning, 1918; Goodyear *et al.*, 1972; Hulley, 1981, 1984; Stefanescu and Cartes, 1992).

CONCLUSIONS

The results obtained in the present study demonstrate the existence of a series of meristic differences (in gillrakers and AOa counts and, to a lesser extent, in dorsal and anal fin rays counts) between the Mediterranean *L. crocodilus* and the Atlantic examples considered at present to be the same species.

The absence of genetic interchange through the Strait of Gibraltar allows them to be considered as distinct species:

LAMPANYCTUS CROCODILUS (RISSO, 1810)

Gasteropelecus crocodilus Risso, 1810: 357 (orig. descr.: off Nice, Mediterranean). No type material available.

Diagnosis

A species of *Lampanyctus* distinguished from all other species in the genus in the North Atlantic Ocean and Mediterranean Sea by the following combination of characters: branchiostegal membrane without minute serial photophores between branchiostegal rays. Three, sometimes two, cheek photophores. Luminous gland at anterior end of base of adipose fin. Total number of gillrakers on first gill arch 15 (14-16). The combination of the high dorsal and anal rays counts, the low number of gillrakers and higher number of AOa photophores, will separate this species from *L. gemmifer*.

Description of meristics

D. 14-15 (13-16); A. 18 (17-19); P. 14 (13- 15); gillrakers 4 (exceptionally 5) + 1 + 10 (9, exceptionally 11), total 15 (14-16); AO 7 (6-8) + 7-8 (9-10), total 15 (13-17).

Distribution

This species occurs only throughout the Mediterranean Sea, both in Western (including Alboran Sea) and Eastern basins.

LAMPANYCTUS GEMMIFER (GOODE & BEAN, 1879)

Scopelus gemmifer Goode & Bean, 1879, *Bull. Essex Inst.*, 11: 22 (orig. descr.: 39° 39'45"N, 71° 35'15"W). Holotype: USNM 35604.

Diagnosis

A species of *Lampanyctus* distinguished from all other species in the genus in the North Atlantic Ocean and Mediterranean Sea by the following combination of characters:

branchiostegal membrane without minute serial photophores between branchiostegal rays. Three, sometimes two, cheek photophores. Luminous gland at anterior end of base of adipose fin. Total number of gillrakers on first gill arch 17 (16-18). This species is distinguished from *L. crocodilus* by its higher gillrakers counts, and also by lower number of the dorsal and anal fin rays and AOa photophores counts.

Description of meristics

D. **14** (13-15, exceptionally 12); A. 17-**18** (16); P. 14 (**13**-15); gillrakers **5** (rarely 4) + **1** + 11 (10-**12**), total 17 (16-**18**); AO 6 (**7**) + 8-9 (7-**10**), total 14 (13-**17**). Numbers in bold type refer to counts of the *L. gemmifer* holotype.

Distribution

This species occurs only in the North Atlantic (including the Gulf of Cadiz), between 33° and 65° N, but with a marked decrease in abundance south of 54° N (eastern sector). It has also been recorded from the Mauritanian upwelling and Cape Islands region, between 15° and 22° N (Nafpaktitis *et al.*, 1977; Hulley, 1981; 1984). All specimens recorded from the Atlantic and identified as *L. crocodilus* (e.g., Krefft and Bekker, 1973) should be considered as belonging to *L. gemmifer*.

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